

Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects

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The cognitive and neural mechanisms underlying category-specific knowledge remain controversial. Here we report that, across multiple tasks (viewing, delayed match to sample, naming), pictures of animals and tools were associated with highly consistent, category-related patterns of activation in ventral (fusiform gyrus) and lateral (superior and middle temporal gyri) regions of the posterior temporal lobes. In addition, similar patterns of category-related activity occurred when subjects read the names of, and answered questions about, animals and tools. These findings suggest that semantic object information is represented in distributed networks that include sites for storing information about specific object attributes such as form (ventral temporal cortex) and motion (lateral temporal cortex).

Studies of patients with focal brain damage suggest distinctions in the cortical representation of objects from different semantic categories. The most frequently documented distinction is between living and non-living things (for example, animals and tools; see refs. 1, 2 for critical reviews). Previous neuroimaging studies examining this distinction have reported greater activity in occipital cortex for animals than for tools^{3–5}. Converging evidence in support of this finding has recently been provided by a study of patients with focal cortical lesions⁶. Although these findings are consistent with the argument that distinctions among different animals depend on access to information about subtle differences in visual features (for example, ref. 2), it is nevertheless surprising to find category-selective activity so early in the visual processing stream. We have previously suggested that this result may be due to top-down modulation of early visual areas by more anterior sites in the ventral, object-processing pathway⁴. If so, then there also should be category-selective activity farther along the object-processing stream to drive this process. Consistent with this idea are reports of patients with damage to ventral temporal cortex, often as a result of herpes simplex encephalitis, who are significantly more impaired at naming and retrieving information about animals than about tools and other manipulable, man-made objects^{7–9}.

Activation of posterior ventral temporal cortex has been reported in positron-emission-tomography studies of object naming^{4,5,10,11}, word reading^{10,12} and semantic association^{13,14}. However, no region in ventral temporal cortex has been identified that responds more in semantic tasks involving pictures of animals than tools. Instead, the most common category-related finding in posterior temporal cortex has been in the opposite direction (greater for tools than animals) and centered on the lateral, rather than the ventral surface (left middle temporal gyrus)^{4,15–19}.

In contrast, functional magnetic resonance imaging (fMRI) studies have reported category-related dissociations in the posterior ventral temporal cortex for a variety of other object cate-

gories, including faces^{20–24}, houses/buildings^{24–26}, letter strings^{20,27} and chairs²⁸. These results suggest that the increased spatial resolution provided by fMRI may reveal previously unobserved category-related dissociations for processing animal and tool stimuli in this region. In the current study, we investigated the functional neuroanatomy of category specificity for animals and tools using a large corpus of stimuli, concentrating on the posterior temporal cortex. Pictures of faces and houses also were included to provide anchor points for evaluating the location of activations associated with animal and tool stimuli. Our findings show a consistent pattern of category-related activity across tasks and individual subjects in both the ventral and lateral surfaces of posterior temporal cortex. Moreover these differences were similar regardless of whether the stimuli were pictures of objects or their written names.

RESULTS

Behavioral data collected during scanning documented that there were no significant differences in reaction time (mean \pm s.e., 725 \pm 27.0 ms; 767 \pm 27.5 ms) or accuracy (percent correct, 97 \pm 1.4%; 95 \pm 1.2%) between animal and tool stimuli used in the matching task. The animal and tool stimuli used in the naming study were equated for naming time (963 \pm 17.0 ms; 989 \pm 12.5 ms) and accuracy (95 \pm 0.8%; 94 \pm 0.7%) as determined by a separate study (n = 12, none of whom participated in the imaging studies).

All subjects showed differential, category-related activations by fMRI. Animal stimuli produced a greater response than tools in two regions of occipital cortex. One of these regions was located medially, centered on the calcarine fissure; the other was located more laterally and inferiorly in the inferior occipital gyrus (Table 1).

Category-related activity also was found further downstream in posterior temporal cortex for both animal and tool stimuli during viewing, matching and naming. Relative to tools, animal

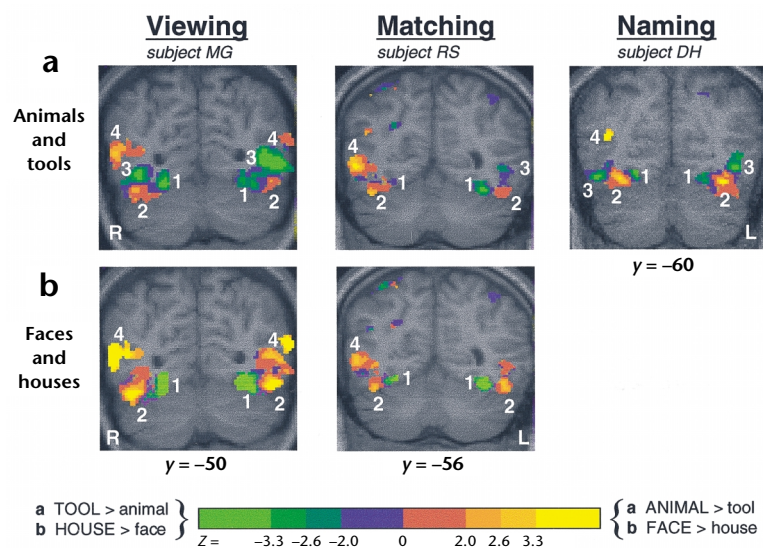


Fig. 1. Examples of category-related activations in three representative subjects. Category-related activations associated with animals and tools (**a**) and faces and houses (**b**) during viewing, matching and silent naming tasks. Talairach and Tournoux coordinates⁵⁰ for the coronal sections are indicated below the images. Voxels displayed in color demonstrated an overall experimental effect ($Z > 3.09$). The color of each voxel reflects an independent test of the significance of the contrast between animals and tools or between faces and houses. Animal- and face-responsive regions are in the red–yellow color spectrum; tool- and house-responsive regions are in the blue–green spectrum. Note that the data sets for viewing, matching and naming tasks are independent, yet they demonstrate remarkable agreement on the locations of borders between animal-responsive (2, lateral fusiform gyrus; 4, superior temporal sulcus) and tool-responsive (1, medial fusiform; 3, middle temporal gyrus/inferior temporal sulcus) regions.

stimuli elicited significantly greater bilateral activation in the lateral region of the fusiform gyrus including the occipitotemporal sulcus (Table 1 and Fig. 1a). Pictures of faces also produced a robust response in this region of the fusiform gyrus (Table 2 and Fig. 1b). In contrast, relative to animals, tool stimuli elicited significantly greater bilateral activation in the medial portion of the fusiform gyrus, including the collateral sulcus (Table 1 and Fig. 1a). Pictures of houses also elicited a robust response in this region (Table 2 and Fig. 1b).

In addition to this general clustering of biological objects (animals, faces) in the lateral fusiform gyrus and non-biological objects (tools, houses) in the medial fusiform gyrus, there were finer-grained distinctions among these object categories. Specifically, the response to human faces was consistently more focal than the response to animals. Thus, whereas both categories of objects elicited a strong response in the lateral region of the fusiform gyrus (Fig. 2a), pictures of animals also produced a significant response in the more medial region of the fusiform gyrus whereas faces did not (Fig. 2b; percent signal change, viewing animals, 0.2%; faces, –0.2%; animals versus faces, $p < 0.0001$; matching animals, 0.7%; faces, 0.4%; animals versus faces, $p < 0.003$). Similarly, direct comparison of the response to tools and houses revealed a consistent, category-related differentiation in the medial portion of the fusiform gyrus. In eight of nine subjects who showed differential responses to both tools and houses, the voxels that responded preferentially to tools were lateral to the voxels that responded preferentially to houses (Fig. 3).

The lateral surface of the posterior temporal cortex also demonstrated differential responses to animal and tool stimuli

for all tasks. Relative to tools, animal stimuli activated a region in posterior superior temporal sulcus (STS; Table 1 and Figs. 1a and 2c). This response was more common in the right hemisphere. Pictures of human faces also activated this region (Table 2 and Fig. 1b). Once again, the neural response associated with animals and faces were similar but not identical. Pictures of animals elicited a stronger response than faces in the more inferiorly located middle temporal gyrus (percent signal change, viewing animals, 0.5%; faces, 0.3%; animals versus faces, $p < 0.0001$; matching animals, 0.7%; faces, 0.3%; animals versus faces, $p < 0.0001$; Fig. 2d). Therefore, as in the ventral temporal cortex, the response to faces was more focal than the response to animals.

In the middle temporal gyrus, tool stimuli elicited significantly greater activation than animals for all tasks (Figs. 1a and 2d). This response was more common in the left hemisphere. In contrast, pictures of houses produced the least amount of activity in the middle temporal gyrus relative to the other object categories (0.2% activation versus 1.1% for tools, 0.5% for animals, 0.4% for faces; Fig. 2d) and failed to elicit activity in STS (0.02% activation versus 0.6% for faces, 0.7% for animals, 0.2% for tools; Fig. 2c).

If these category-related activations identify regions where we store information about critical object properties^{2,29}, then words representing these objects also should activate these regions. To test this idea, subjects were required to read and answer general questions about the written names of animals and tools. This task produced a topological arrangement of activations similar, in part, to the pattern associated with naming pictures of objects from these categories. Reading the names of and answering questions about animals activated the inferior region of the occipital lobe, lateral fusiform gyrus and left STS. In contrast, reading the names of and answering questions about tools activated the medial fusiform gyrus and the left middle temporal gyrus (Table 1 and Fig. 4a). In addition, voxels in the right lateral fusiform gyrus that were significantly more active when subjects answered questions about animals also showed a greater response when subjects named animal pictures ($p < 0.05$). Similarly, voxels in the right medial fusiform and left middle temporal gyri that were significantly more active when subjects answered questions about tools were also more active when subjects named pictures of tools ($p < 0.05$; $p < 0.0001$ for right medial fusiform and left middle temporal regions, respectively; Fig. 4b). These were the only voxels significantly active in both tasks.

DISCUSSION

The results of these studies documented a consistent pattern of category-related activations in the posterior cortex across a variety of different tasks. First, as reported in previous neuroimaging studies^{3–5}, photographs of animals elicited greater activity in the medial occipital cortex than did photographs of tools. In addition, animals produced greater activity in the inferior occipital gyrus than tools. Because the inferior occipital activity occurred in response to both photographs of animals and their written names, it cannot be attributed to the greater visual complexity of the animal stimuli relative to tools. This finding is consistent with the

Table 1. Regions showing differential responses to animals (A) and tools (T).

Region	Selectivity	Task (n/N)	Hemisphere (n)	Talairach coordinates (x,y,z)
Occipital lobe				
Medial occipital region	A > T	viewing (5/8)	R (5)	15, -92, 1
			L (3)	-9, -88, 9
		matching (4/4)	R (4)	12, -87, -7
			L (1)	-17, -97, -16
		naming (6/14)	R (5)	15, -93, -1
			L (3)	-11, -96, 2
Inferior occipital gyrus	A > T	reading (0/8)	R (0)	— — —
			L (0)	— — —
		viewing (7/8)	R (7)	33, -84, -5
			L (4)	-30, -81, -1
		matching (3/4)	R (3)	29, -84, -11
			L (3)	-36, -78, -15
Ventral temporal lobe	A > T	naming (12/14)	R (12)	41, -80, -10
			L (9)	-36, -80, -10
		reading (5/8)	R (3)	31, -76, -15
			L (2)	-29, -72, -18
		viewing (6/8)	R (6)	38, -56, -12
			L (4)	-40, -59, -10
Lateral fusiform gyrus	A > T	matching (2/4)	R (2)	41, -53, -20
			L (1)	-35, -59, -20
		naming (14/14)	R (14)	37, -52, -20
			L (12)	-37, -55, -20
		reading (6/8)	R (5)	37, -55, -21
			L (4)	-40, -56, -21
Medial fusiform gyrus	T > A	viewing (6/8)	R (4)	26, -48, -9
			L (6)	-26, -47, -5
		matching (3/4)	R (1)	32, -65, -19
			L (3)	-26, -53, -17
		naming (13/14)	R (8)	26, -47, -16
			L (13)	-27, -50, -15
Lateral temporal lobe	A > T	reading (6/8)	R (4)	23, -59, -11
			L (3)	-32, -53, -17
		viewing (4/8)	R (4)	53, -54, 16
			L (1)	-42, -59, 19
		matching (2/4)	R (2)	43, -61, 12
			L (0)	— — —
Superior temporal sulcus	A > T	naming (6/14)	R (5)	52, -59, 15
			L (2)	-43, -63, 8
		reading (2/8)	R (0)	— — —
			L (2)	-64, -40, 6
		viewing (6/8)	R (3)	40, -53, 0
			L (6)	-46, -55, 3
Middle temporal gyrus	T > A	matching (3/4)	R (1)	46, -56, 4
			L (3)	-47, -54, 6
		naming (12/14)	R (1)	50, -54, 6
			L (12)	-45, -57, 7
		reading (7/8)	R (0)	— — —
			L (7)	-49, -52, -3

N, total number of subjects tested; n, number of subjects who showed significant, category-related activation ($p < 0.05$).

idea that retrieving information about objects that are differentiated primarily by differences in visual form (that is, four-legged animals) requires top-down activation of visual processing areas. Within this context, our finding of a region in the ventral temporal lobe that responded more strongly to animals than tools may provide a neural basis for selective semantic deficits for animals and other living things following temporal lobe lesions^{7–9}, possibly as a consequence of disrupted function of this area and its feedback connections to occipital cortex³⁰.

Within the fusiform gyrus, different activation patterns were noted for each object category tested. Previous studies of object naming^{4,5,10,11}, word reading^{10,12} and semantic association^{13,14} have activated this region of ventral temporal cortex (~4.5–6 cm posterior to the anterior commissure). The present fMRI data not only confirmed the importance of this region for semantic processing, but also revealed category-related activations that were highly consistent across individual subjects and processing tasks.

The more lateral aspect of the fusiform gyrus responded more to animals than to tools. Consistent with other reports, this region also responded strongly to human faces^{20–24}; however, the fusiform activations associated with faces and animals were not identical. In particular, animals elicited a stronger response in the medial fusiform gyrus than did faces. This finding suggests that although animal and face recognition may depend, at least partially, on a common neural substrate, faces may be processed by a more discretely organized system. This finding, in turn, may provide a neural basis for why prosopagnosia, or the inability to recognize faces, can occur as an isolated disorder in some patients³¹ and also why difficulty identifying four-legged animals is a common, perhaps the most common, co-occurring symptom in prosopagnosic patients³².

Similarly, and again consistent with recent reports^{24–26}, the medial fusiform region that responded strongly to tools also responded strongly to houses. However, as was the case for the animals and faces, direct comparison of houses and tools revealed finer-grained distinctions between these object categories as well. The peak activity associated with tools was consistently lateral to the peak activation associated with houses. These findings suggest that the pattern of response to different object categories varies continuously across the posterior ventral temporal cortex. For this reason, we believe the ventral temporal cortex may be organized according to object features that cluster together^{28,29}. The nature of these features remain to be determined. However, because the fusiform gyrus is part of the ventral object-vision pathway³⁰, one likelihood is that this region is tuned to features of object form shared by members of a category.

A consistent, category-related topology was also found along the lateral surface of posterior temporal cortex. Previous studies with human^{33,34} and nonhuman primates^{35,36} have demonstrated that posterior STS responds to biological motion (for example, mouth and eye movements). The finding that animals and human faces elicited greater activity in posterior STS than tools and houses suggests that the posterior STS may be involved not only in the perception of biological motion, but also in storing information about biological motion.

Similarly, the posterior middle temporal gyrus may be a site for stored information about non-biological object motion⁴. This idea is supported by the proximity of this area to motion perception areas³⁷ and by its selective activation when subjects generate action words^{38–40} and name and retrieve information about tools^{4,15–19}. Finally, damage to this area has been linked to a selective loss of knowledge about tools⁶.

Thus, as we suggested for the ventral temporal lobe, the lateral region of the temporal lobe may also be tuned to different

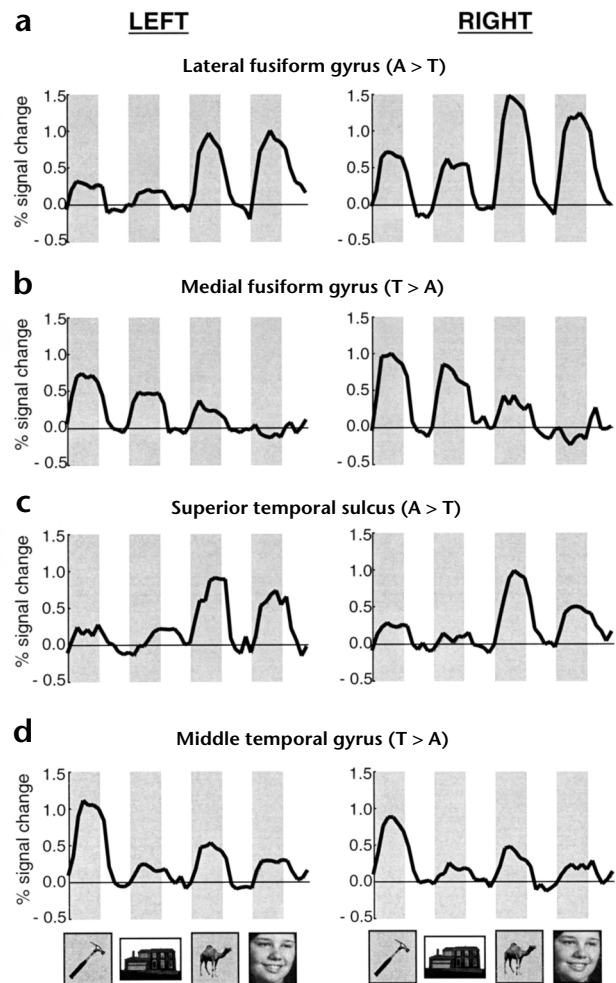


Fig. 2. Amplitude and time course of category-related modulation. Representative mean time series for lateral fusiform gyrus (a), medial fusiform gyrus (b), superior temporal sulcus (c) and middle temporal gyrus (d) from the contrast between animals (A) and tools (T) in the viewing task. Data were averaged over subjects and all stimulus categories. Gray bars indicate presentation of meaningful stimuli, and intervening white areas indicate presentation of control stimuli (phase-scrambled images of the objects).

object features that members of a category share. Although the nature of these features also remain to be determined, given the functional properties of posterior STS and middle temporal gyrus discussed above, one possibility may be that the lateral temporal cortex is tuned to the features of object motion. Biological objects (faces and animals) were associated with heightened activity in STS, whereas tools were associated with heightened activity in the middle temporal gyrus. Houses, which by definition are stationary, produced negligible activity in both regions. This pattern of activation suggests a superior-to-inferior gradient that may be tuned to the features yet to be determined that distinguish biological motion from motion associated with the use of manipulable, man-made objects.

Reading the names of, and answering questions about, animals and tools also produced category-related activity in some of the same regions identified by the picture processing tasks. This correspondence provides strong evidence that activity in posterior temporal cortex reflects stored information about an

Table 2. Posterior temporal regions showing differential responses to faces (F) and houses (H).

Region	Selectivity	Task (n/N)	Hemisphere (n)	Talairach coordinates (x,y,z)
Ventral temporal lobe				
Lateral fusiform gyrus	F > H	viewing (7/8)	R (7)	39, -59, -11
			L (7)	-39, -55, -8
		matching (8/10)	R (8)	39, -53, -19
			L (8)	-39, -54, -18
Medial fusiform gyrus	H > F	viewing (8/8)	R (8)	27, -53, -9
			L (6)	-29, -52, -6
		matching (9/10)	R (9)	25, -50, -12
			L (9)	-27, -52, -12
Lateral temporal lobe				
Superior temporal sulcus	F > H	viewing (4/8)	R (4)	53, -54, 16
			L (1)	-42, -59, 19
		matching (4/10)	R (4)	51, -55, 12
			L (2)	-48, -57, 9

N, total number of subjects tested; n, number of subjects who showed significant, category-related activation ($p < 0.05$).

object, not just the physical features of the material presented for processing. Moreover, the finding that an area assumed to be involved in storing information about object form (fusiform gyrus) was the region most active when subjects read and answered questions about animals is consistent with the argument that information about visual object form is critical for distinguishing among different animals². Similarly, the finding that a region assumed to be involved in storing information about object use-associated motion (middle temporal gyrus) was most active when subjects read and answered questions about tools is consistent with the idea that functional information, such as object use-associated motion, is critical for distinguishing among different tools.

These findings suggest that thinking about a particular object may require activation of the critical features that define that object. Thus, thinking about any characteristic of a particular animal would require activation of visual feature information (as evidenced by the selective activation of the lateral fusiform region during animal name reading). This finding could provide an explanation for why some patients with a category-specific disorder for recognizing living things have difficulty answering questions that probe both visual and nonvisual information^{1,41-44}. In this view, these patients have damage to regions of the brain that store information about the visual form of animals, and activation of these representations may be necessary to gain access to other types of information about animals, assumed to be stored elsewhere. Neuroimaging evidence in support of

this possibility has been reported⁴⁵.

In contrast, it has been proposed that semantic knowledge is organized according to evolutionarily adapted, domain-specific knowledge systems for biological and non-biological kinds¹. The clustering of activations associated with animals and faces, on the one hand, and tools and houses, on the other, may be viewed as consistent with this interpretation, with the added stipulation that there are finer-grained distinctions that reflect the neural representation of different types of biological and non-biological objects¹. However, evidence suggests that not all representations of non-biological objects cluster together. For example, we have

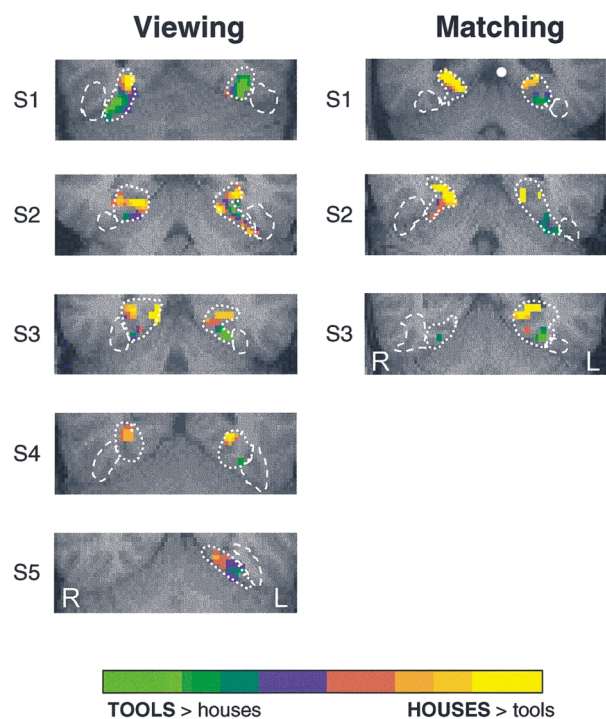


Fig. 3. Category-related activations during tool and house perception in voxels that responded to both stimuli in the medial fusiform region. Nine of twelve subjects (eight viewing, four matching) showed a differential response to both tools and houses. Eight showed the same topological arrangement. Note that the voxels that responded preferentially to tools (blue–green spectrum) are lateral to the voxels that responded preferentially to houses (red–yellow spectrum). White dotted lines represent the borders of the medial fusiform region that responded more to pictures of tools than to pictures of animals; white dashed lines represent the borders of the lateral fusiform region that responded more to animals than to tools.

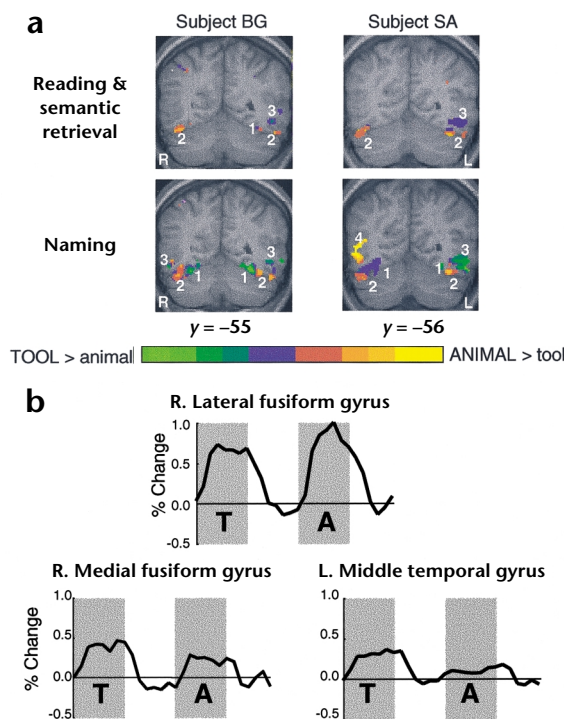


Fig. 4. Pictures and words elicit common category-related activations. **(a)** Category-related activations during the word reading/semantic retrieval task and the picture naming task in two representative subjects. Talairach coordinates for the coronal sections are indicated below the images. Note that the topological arrangement of the animal-responsive (2, lateral fusiform gyrus) and tool-responsive (1, medial fusiform; 3, middle temporal gyrus/inferior temporal sulcus) regions for the reading task is similar to the topological arrangement of these regions for the naming task. **(b)** Mean time series for voxels that were active during both word reading and picture naming. Voxels were identified by contrasting the animal and tool conditions during the reading task. The response to naming pictures of animals and tools was then evaluated in these reading-defined voxels.

reported that the peak of activity associated with chairs, a category of objects with no evolutionary significance, was located lateral to the face-responsive region (in the inferior temporal gyrus), rather than medially²⁸. Moreover, the domain-specific hypothesis does not make any predictions about where information about biological and non-biological objects is represented in the brain. The present data, along with other neural imaging findings^{17–19} indicate first that object knowledge is stored as a distributed network, and second that the location of these sites are not randomly distributed, but rather mirror the organization of sensory and motor systems^{4,40}. (See ref. 2 for review of similar models.) Studies showing selective activation of left premotor cortex for naming^{4,46} and retrieving information about tools⁴⁷ provide additional support for this view. Whether there is a broader organization of these networks reflecting evolutionarily adapted, domain-specific knowledge system for biological and non-biological kinds remains to be determined.

In summary, the results of these studies suggest that object knowledge is stored as a distributed network of cortical regions that prominently includes the posterior regions of the ventral and lateral temporal cortex. Our ability to think about and identify different categories of objects may depend on the activation

of stored information about the critical sensory- and motor-based properties that define an object and distinguish it from other members of the same category²⁹.

METHODS

Experimental design. The stimuli were black-and-white photographs of animals, tools, faces and houses and the printed names of animals and tools. All the tasks were presented in a block design. For the viewing task, 1732 different stimuli were used (432 photographs per category). The stimuli were presented at fixation at a rate of 2 per s, and subjects were instructed to look carefully at each picture. For the matching task, 240 different stimuli were used (60 photographs per category). A sample stimulus was presented for 1 s. Following a 0.5-s delay, 2 choice stimuli (different exemplars of the same object) were presented side by side for 2 s. Subjects indicated which object was identical to the sample stimulus with a button press. For the naming task, 360 different stimuli were used (6 exemplars of 30 namable animals and tools, matched for frequency and for voice onset time). The stimuli were presented at fixation for 2 s, and subjects silently named each object. None of the stimuli were repeated for the viewing, matching or naming tasks. For the reading task, the written names of animals and tools were presented for 2 s at fixation, and subjects silently read each word. To ensure that subjects read the words, general yes or no questions preceded each block (for example, a block of animal names was preceded by “Forest animal?”; a block of tool names by “Kitchen tool?”). Subjects responded with button presses. There were 134 different animal names and 133 different tool names. A small subset of the words were repeated so there would be an equal number of stimuli in each block.

Subjects. Twenty-six neurologically normal, right-handed subjects participated in these studies. All subjects gave written informed consent in accordance with procedures and protocols approved by the NIMH Institutional Review Board. Eight subjects participated in the viewing task, four participated in the matching task, and six participated in the naming task. (These six subjects also performed a matching task with photographs of faces and houses.) Eight subjects participated in the reading/semantic retrieval task. These eight subjects also performed a naming task with photographs of animals and tools. Subjects always performed the reading/semantic retrieval task first so reading would not be influenced by the pictorial examples.

Imaging. There were six imaging runs for each task. Run duration was 5 min, 24 s for the viewing and matching tasks and 4 min, 48 s for the naming and reading tasks. Eighteen contiguous, 5-mm-thick coronal images of posterior cortex were obtained on a 1.5 Tesla GE Signa scanner using standard imaging procedures (TR = 3 s, TE = 40 ms, flip angle = 90°, FOV = 20 cm, 64 × 64 matrix) as described²⁴.

Data analysis. Individual subject data were analyzed using multiple regression^{48,49}. Images were smoothed within the coronal plane using a Gaussian filter with a full width at half maximum of 1.2 voxels (3.75 mm). Changes in neural activity were modeled as square-wave step functions coincident with the end of one stimulus block and the beginning of another. These changes were decomposed into orthogonal contrasts: the differences between animals and tools and between faces and houses. Additional contrasts tested for differences between tools and houses and differences between animals and faces. The square-wave contrasts were convolved with a Gaussian model of the hemodynamic response using experimentally derived estimates of lag (4.8 s) and dispersion (1.8 s). These convolved contrasts were the regressors of interest in the multiple regression analysis. Additional regressors of no interest were included in the analysis to partial out variance due to differences in mean intensity between imaging runs and linear changes in intensity within runs.

To identify brain regions that responded to visually presented objects, we selected voxels that showed a significant experimental effect ($z > 3.09$ for the combined effect of the regressors of interest) and an overall increase in activity for objects. Next, category-selective regions were identified as clusters of 7 or more voxels that showed a differential response to animals versus tools or faces versus houses ($z > 1.96$, $p < 0.05$, two-tailed).

Stereotaxic coordinates⁵⁰ were obtained for each of these regions. (See ref. 24 for details.) A mean time series was calculated for each region of activation in each subject. Multiple regression with orthogonal contrasts was used to test the significance of differences across all subjects.

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